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AN ADVENTURE IN ADAPTATION: The European Corn Borer, *Ostrinia Nubilalis (Hubn.)*

C. R. Neiswander

OHIO AGRICULTURAL EXPERIMENT STATION
Wooster, Ohio

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The European corn borer was first found in Ohio in 1921 in a narrow strip of land along the southern shore of Lake Erie. It spread southward and westward at the rate of 12 to 15 miles per year in spite of concentrated efforts at quarantine and control. By 1927 the corn borer was present over the northern half of the State of Ohio and by 1938 it occurred throughout the State as well as in much of northern Indiana and northeastern Illinois (Figure 1). At the present time it occurs over practically all of the eastern half of the country except the extreme southeastern and southern portions. Its area of distribution now includes all of what is known as the great corn belt of the United States (Figure 2).

Inasmuch as research workers and farmers in Ohio have now lived with the insect for a period of nearly 40 years, it might be of interest to review its history over this period and see how it has behaved in its new home.

The corn borer is thought to have entered Ohio from Ontario across Lake Erie inasmuch as the insect was first found along the shore of the lake and since it was known to have been present in Ontario several years previously. During the time of its early occurrence in Ohio, the species was creating havoc in the corn growing section of Ontario. Few insects have laid waste fields more completely than the corn borer did Canadian corn during the period 1924 to 1927. As a result of its depredations, corn acreage in the severely infested area was reduced to about 35 per cent of normal, sweet corn canners ceased to operate, and land values dropped. In those days the only really effective control measure known was the destruction of the crop residues which harbored the overwintering borers. In Canada this was not an insurmountable task, but in the corn section of our midwest, it seemed essentially impossible. As far as the use of agricultural chemicals was concerned at that time, it seemed completely impractical to consider the treating of corn fields with insecticides. There were no chemicals available that offered hope and, even if there had been, there was no equipment available for making application. It was this situation that caused agriculturists to view the introduction of the corn borer into Ohio with consternation.

In 1926 one of the leading entomologists of the Central States Region of the United States made the following statement: "The European corn borer is beyond doubt the most menacing insect pest ever introduced into North America since it threatens in no uncertain manner our basic agricultural product – Indian corn. If it continues to accumulate as we have every reason to expect, we are on the verge of a national calamity."

Figure 1.–Rapidity of spread of the corn borer across the State of Ohio.

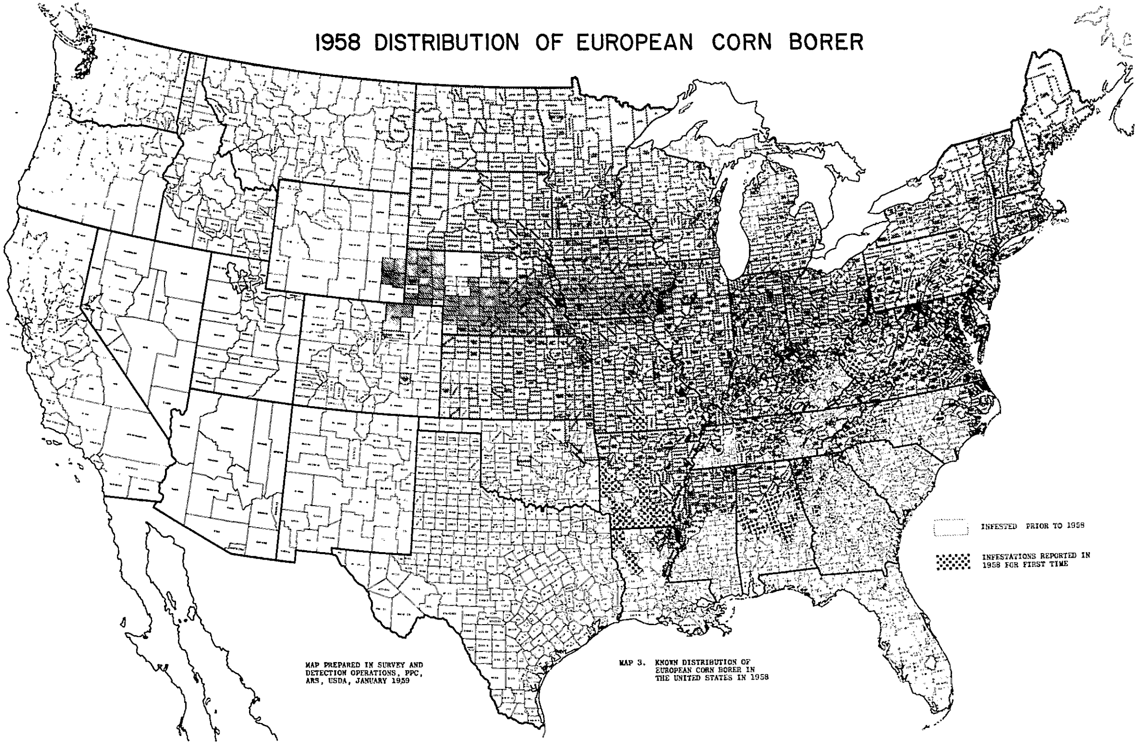

Figure 2.—Distribution of the corn borer in the United States at the end of the 1958 season. (Cooperative Economic Insect Report Vol. 9, No. 5, p. 62).

That was the opinion of many of the leading agriculturists of the day who were familiar with the progress of the insect up to that time.

Yet, the greatest yields of corn the State of Ohio has ever produced have been harvested during the past five years. As a matter of fact, there has been a phenomenal and steady increase in per acre corn production throughout the past 30 years as shown in Figure 3. It may be noted that at the beginning of the borer era there was an average per acre production in Ohio of 34.6 bushels. For the most recent period it was 60.2. This amounts to an overall increase of nearly 75 per cent for the period. These are not isolated experimental results but estimated annual corn production records as taken from accumulated agricultural statistics.

This is not to say that the corn borer is no longer causing damage in the United States or in Ohio. The estimated corn loss from borer injury in the United States for 1958 was $98,434,000 and for 1957, $158,841,000.

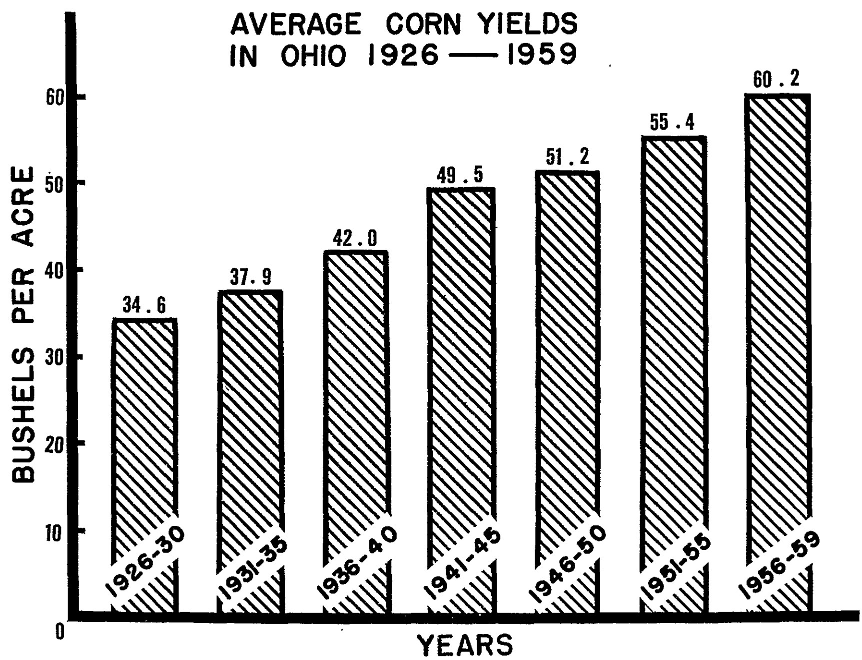

Figure 3.—Average corn yields in Ohio 1926-1959. (From Ohio Agricultural Statistics. See Literature Cited.)

For the corresponding years the Ohio losses were $2,557,000 and $1,450,000. (These records are from the Cooperative Economic Insect Report for January 31, 1958 and April 24, 1959). These look like impressive figures when published alone, but in Ohio a $2,000,000 loss on a $200,000,000 production value still represents only about one per cent of the crop. It is doubtful if this loss could have been greatly reduced economically even with intensive control effort. At any rate Ohio farmers at the present time are not greatly concerned about corn borer losses.

What has happened to the corn borer that it has failed to live up to the dire predictions that were made at the time of its introduction? Have the climatic conditions been inimical? Has the cropping procedure been revolutionized to the extent that corn crop remnants are now largely destroyed and that as a result but few hibernating borers are now available for reinfestation? Have strains of hybird corn been developed on which the insects have been unable to feed and survive? Have insect parasites or have other biological enemies served to prevent the complete expression of the destructive powers of the species? Has the recent phenomenal development of new agricultural chemicals and techniques in their application served to keep infestations at low levels? In short, has the species failed to become adapted to the Ohio enviroment or have manipulated adjustments in the environment that were inimical to the insect prevented full expression of its potentiality?

These are academic questions that cannot be answered specifically. The problems mentioned and many others have been and are still being studied intensively by both state and federal investigators. Many modifications of the corn production program have been made as a result of these investigations.

In early corn borer years new farm machinery was developed for the disposal of crop residues. This machinery aided in the control program by killing large numbers of hibernating borers. Yet, in 1927 a $10,000,000 cleanup or crop disposal campaign that was intended to reduce the borer population to near the zero point if not eliminate the species completely from our region failed to do more than cause a slight and temporary retardation in the accumulation and spread of the insect. In recent years the increased use of the corn picker has favored corn borer accumulation in that crop residues containing borers are now largely left in the field.

Perhaps the most effective cultural operation recommended as a corn borer control procedure in the past was delayed planting, During the first 15 years after the introduction of the insect, farmers in northwestern Ohio could be relatively certain that severe corn borer injury would not occur if planting was delayed until May 25. However, if planting was purposely delayed until May 25 and then a week of rainy weather caused a further delay of a week, as sometimes happens, the planting became too late for maximum corn yields. In recent years producers of dent corn have tended to ignore the delayed planting recommendation because they are no longer greatly concerned about corn borer injury to early planted corn.

During the 40 years that have elapsed since the corn borer was introduced into the state, the use of corn varieties has been revolutionized. Corn hybrids that were first grown commercially in the early 1930's have so completely replaced the old open-pollinated varieties that today it is difficult to obtain seed of many of the old varieties even for experimental purposes.

In Ohio intensive efforts have been devoted to the study of corn strain resistance to corn borer injury in the hope of developing good commercial hybrids on which the borers would not do enough feeding to cause important damage. Although no hybrid completely immune to corn borer injury has ever been produced, corn hybrids do exhibit great variability in their susceptibility to corn borer injury. Hybrids have been developed in which corn borer feeding has been slight when others were severely damaged (Figure 4). As a consequence, in areas of high corn borer accumulation, growers have been advised to plant the more resistant hybrids. Some growers have adopted these recommendations and no doubt in so doing have reduced the potential for corn borer damage in their respective localities. There is no doubt that the continuing development of new and better corn hybrids has been in a large measure responsible for the phenomenal increase in acre corn production that has occurred during the past 30 years.

A few years ago one of the prominent entomologists of the country made the statement in an article in The Scientific Monthly that "In northwestern Ohio, where the European corn borer has been prevalent, it would no longer be possible to grow corn commercially if borer resistant hybrids had not been developed". Such a statement must have been based on the assumption that since fields of corn have been devastated by borer injury in the past and are not devastated now the differences must be due to the differences in the strains of corn used. That this statement is obviously incorrect is evidenced by the fact that some hybrids are grown in northwestern Ohio that are even more susceptible than were many of the old open-pollinated varieties. In fact, four hybrids grown in Ohio today, namely, Ohio K35, Indiana 252A, Iowa 4059, and

Iowa 4297, are highly susceptible to corn borer injury. The reason such hybrids are grown is that they have other qualities that farmers like sufficiently well to cause them to risk the chance of corn borer injury. When severe corn borer damage does occur, farmers tend to avoid such hybrids the following year.

In like manner the use of fertilizers has undergone a marked change. Not only has fertilizer usage been greatly expanded but farmers have learned to select and use fertilizers on the basis of crop and soil needs and they have also learned how to place fertilizers in the soil for maximum benefit. An increase in fertilizer usage has led to an increase in the number of plants per acre. Whereas 30 years ago farmers were growing 8,000 to 10,000 plants per acre many of them are now growing as many as 15,000 to 18,000.

There is no doubt that the improvement in fertilizer usage has greatly increased corn production. However, in no sense has the fertilizer program contributed to corn borer control. Inasmuch as corn borer moths

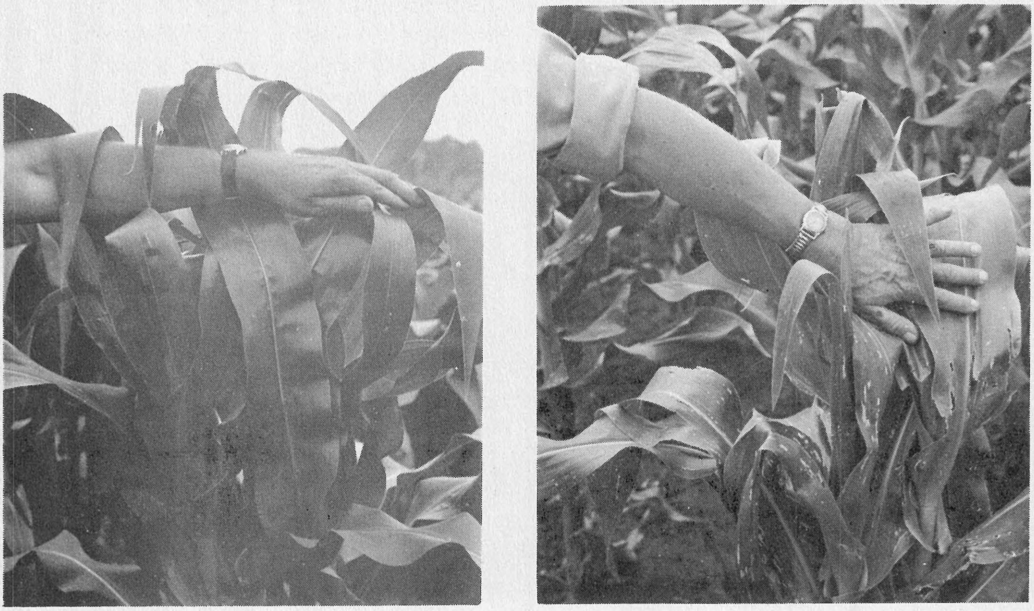

Figure 4.–Two hybrids showing differential corn borer injury from same number of egg masses. Plant on left resistant, on right susceptible. (Courtesy of F. F. Dicke)

are attracted to the most luxuriantly growing corn in an area, the use of an optimum fertilizer program would tend to increase the intensity of corn borer infestation.

A number of corn borer parasites including both dipterons and hymenopterons have been introduced from Europe and have been released at various points in the state. In some localities as many as 35 per cent of the borers are known to have been killed by these introduced parasites. Also, some of our native beneficial insects, such as ladybird beetles and and many predaceous mites, annually take a toll of corn borer eggs and larvae. Birds, such as the downy woodpecker, consume considerable numbers of corn borer larvae during the fall and winter in local areas. Yet few investigators consider any of these agents of biological control of major importance in the corn borer control program today. It is probable that their real value is underestimated.

In Ohio the corn borer has usually attained its greatest accumulation in market garden sweet corn sections. In many market garden areas of Ohio early planted and early maturing sweet corns suffered such severe injury that many growers at one time discontinued their attempts to produce crops for the early market. After investigators learned that the insect could be controlled by the application of insecticides and when high clearance machinery became available for treating corn, these growers again produced high quality crops.

Today most of the commercial market garden sweet corn grown in Ohio is treated for corn borer control. On the other hand, the insect has never been able to survive as well in the large-stalked, long-season dent corns, as in the sweet corns or in the short-season and small-stalked dent and flint corns. For this reason the corn borer never has destroyed so completely the tall dent corns of Ohio as it did the flint corn crops of Kent and Essex Counties, Ontario. At the present time very little dent corn in Ohio is treated for corn borer control.

All phases of the investigational program have contributed directly or indirectly to the ultimate goal of producing corn with profit in spite of corn borer infestation. Certainly investigators are justified in maintaining that a considerable portion of our corn crop has been saved from destruction through research in all of its phases. The advent of the corn borer, instead of leading to disaster, can be said to have contributed indirectly to our increased yields of dent corn insofar as it has stimulated research in corn breeding, in improved fertilizer application practices, in insect parasitization, in the use of agricultural chemicals, as well as in farm mechanics, and in other phases of the corn production program.

Throughout its period of existence in Ohio the corn borer has shown great fluctuations in population within a few years' time. Futhermore, the area of most severe damage has shifted from one locality to another, always, however, within Ohio's corn belt area or the western half of the state. The borer population in Ohio for the past 21 years is shown in Figure 5. This is the period during which the insect has been distributed over the entire state. It may be noted that the borer reached its greatest abundance in 1940 and in 1949. In these two years considerable damage was experienced in isolated fields. Although the average loss for the state in those two years was not more than 6 to 10 per cent of the crop, there were a number of fields that had 10 to 15 borers per stalk and the losses in such fields were correspondingly higher. The losses are calculated on the basis of 3 percent for each borer population average of one per stalk. For instance, if the borer population of a given field is estimated at 150 borers per 100 stalks, the loss for that field would be estimated at 4½ percent of the crop. It may be noted from Figure 5 that in only two of the 21 years was the average population for the state as high as two borers per stalk and in most years it was less than one.

Shortly before the year 1938 an important change in the behavior of the insect was noted. During the years from about 1935 to about 1944 the

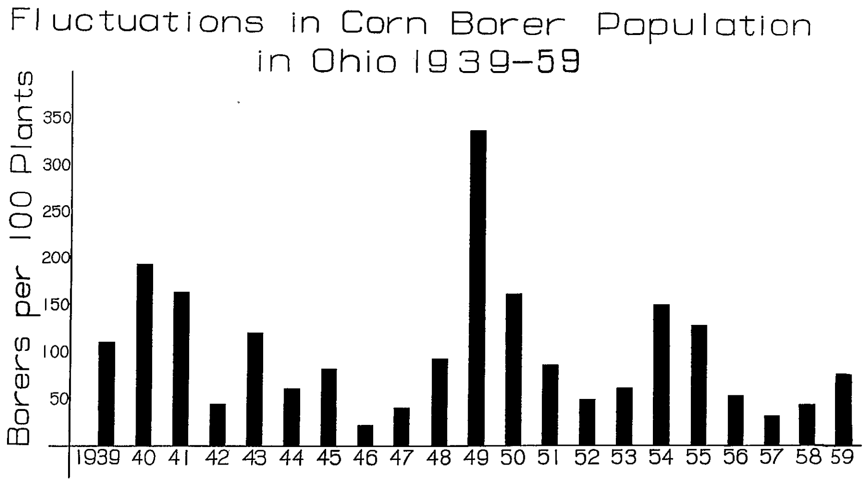

Figure 5.—Borer population levels in Ohio 1939-1959.

insect may be said to have been in a transition stage from a univoltine to a multivoltine type of behavior. These and other accompanying changes may have been of prime importance to the insect and to midwest agriculture.

In order to point out the rather vital changes that have occurred in the life history of the insect, it will be necessary to review its seasonal behavior. For the first 15 years of its existence within our state the insect followed pretty much of a routine schedule. The moths were at the height of their flight during the first week of July. During that period, eggs were deposited on corn the largest of which at the time was about waist high. The larvae that hatched from the eggs fed on various parts of the corn plant and became full grown by late August or early September. Regardless of how early in the season the insects became full grown and regardless of how high the temperature might remain in the fall or how long high temperatures might persist, the insects entered a diapause and failed to transform to moths. Larvae that were taken into the laboratory and kept constantly at high temperatures also failed to transform unless or until they were first subjected to refrigeration. In the field they went into hibernation as full grown larvae within the corn stalks. About the middle on the following June the larvae changed to the pupal stage from which the moths merged in early July. There was always some fluctuation in the time of appearance of the various stages depending upon the weather conditions, but the seasonal rythm continued with only slight modifications for which explanations could be given. There was always a single and complete generation or cycle each year and the moths were always in flight through late June and early July and at no other time[1].

Beginning about 1935 aberrations were noted in this rhythmic cycle. Moths were observed to emerge in August from the current season's larvae. They deposited eggs on corn that was approaching maturity and and the larvae developed into full grown corn borers before cold weather stopped their activity. Within a period of a few years, this phenomenon was observed in widely separated localities. It was observed first in market garden sweet corn areas, but in a short time, it was observed also in dent corn. As stated previously early-planted and early-maturing market garden sweet corns have been particularly susceptible to corn borer injury. From a given number of eggs, a greater number of larvae develop to the full grown stage on the short-season sweet corns than on long-

[1] In the early years after the corn borer's introduction into Ohio an occasional pupa would be seen in the late summer but the occurrence was so rare that it was considered an abnormality and of no consequence.

season dent corns. Today a higher percentage of borers emerge for a second generation from the early sweet corns than from the dent corns.

At the time of the change from the univoltine to bivoltine behavior the insects that were the progeny of the second moth flight were found to emerge from 10 days to 2 weeks earlier during the following spring then had been the standard behavior before the change. Instead of having the major part of the moth flight during the first week of July, the major part of the moth flight of this group of insects occurred between the 20th and 25th of June in northern Ohio.

During this transformation period there was thus a divided moth flight period. That is, the insects that had gone through two generations the preceding year were found to emerge about 10 days earlier than the usual period, whereas the insects that had had but a single generation the preceding year emerged at the usual time. The transition period continued until about 1944 after which there was no longer a divided spring moth flight period. From that year on the entire spring population emerged 10 days to 2 weeks earlier than had been the practice in former years. Apparently as a result of further adaptation to environmental conditions and perhaps the interbreeding of the two groups the entire population came to behave alike as far as the period of spring emergence is concerned.

It should not be understood, however, that the entire corn borer population now goes through two generations per year. It is extremely seldom that all of the borers in any one field emerge as adults during the year of larval feeding and growth. The numbers that do emerge in the fall for a second generation apparently depend on a number of factors. In fields taken at random over the state during recent years, this percentage has varied from near zero to near 100. In general, it has been higher in southern Ohio than in northern Ohio and higher in market garden sweet corn than in field corn. In dent corn the maximum has usually been around 30 to 40 per cent, and in sweet corn 50 to 100 per cent.

It would seem that with the addition of a second generation in any season the possibility of corn borer accumulation would be increased tremendously since there is no intervening winter mortality, or between crop cultural practices, to reduce the population. Yet, the annual borer population level certainly has not shown any important increase. In fact, as far as Ohio is concerned, there has been a decrease in overall borer losses since the transition occurred.

The explanation for the decrease in corn borer losses probably lies in a number of factors. In the first place, the earlier emergence has reduced the chances of borer survival of the first generation as compared to that of the single generation in former years. As stated earlier in this paper, perhaps the most effective recommendation for corn borer control in the past has been delayed planting. This control procedure has been effective from two standpoints. To be highly attractive to ovipositing moths, corn must be above 16 inches high at the time of major moth flight. If the corn is not that high at moth flight, there will be but few eggs deposited upon it. But perhaps more important than this is the fact that the percent survival of borers hatching from eggs placed on the plants varies directly with the nearness of the crop to maturity at the time the eggs are deposited.

The 10 days to 2 weeks advance in the moth flight period, that came with the increase in the number of generations, has therefore been equivalent to a similar delay in corn planting as far as corn borer infestation is concerned. Consequently, early planting is no longer the hazard that it was before the change in corn borer behavior occurred. In recent years the infestations in early planted dent corn have not been as severe as they were some years ago. In early planted market garden sweet corn on the other hand, severe infestations still occur because the crop is usually advanced enough to receive a high proportion of the early eggs deposited and because the period between egg deposition and host maturity in that crop is still sufficiently short to result in a relatively high borer survival.

Now that there are two generations a year the first attacks the early corn and the second the late maturing corn. The bulk of the crop from intermediate plantings has a relatively low infestation which may consist of a mixture of the two generations. The moths are always attracted to vigorously growing fields of corn for oviposition. Inasmuch as the earliest planted corn is usually in the most rapid vegetative stage at the time of the first moth flight, such plantings commonly get the most first generation eggs. By the time of the second moth flight the earlier plantings have passed the attractive stage and eggs accordingly are placed largely on later plantings that are still in a relatively early stage of development. But few second generation eggs are deposited in fields that are approaching maturity.

Larvae of the first generation cause much more damage per individual than do larvae of the second generation because the first generation attacks the crop at a much earlier stage. At the time of the second generation infestation the crop is approaching maturity when insect feeding starts and actual yield loss is less. However, larvae of the second generation can cause extensive stalk breakage and ear droppage and thereby make harvesting more difficult.

Borer population surveys are made by examining representative plants in 10 fields selected at random in each county surveyed. The fall survey is usually made in early October after most of the active insect feeding has stopped. At that time approximately 80 to 90 percent of the borers observed are second generation borers. The other 10 to 20 percent are remnants of the first generation that failed to transform to adults but remained as larvae and therefore make up the univoltine portion of the population.

Estimates of yield losses caused by the borer are based on data tending to show that an average of one borer per stalk will decrease the yield 3 per cent. However, the data for this estimate were taken under single generation infestation more than 20 years ago. Inasmuch as no evaluation of second generation losses has ever been accepted by investigators as a whole, the old 3 per cent evaluation is still used. However, Ohio entomologists are inclined to estimate present day losses in Ohio at only 2 per cent per borer per plant. In that case the loss in 1949 (a second generation population) would be essentially the same as that in 1940 (a single generation population) even though the fall population in 1949 was considerably higher (Figure 5).

The changes that have occurred in corn borer behavior in a relatively short time are extremely unusual. The underlying causes are not clear, although there have been some interesting conjectures.

At the beginning of this paper it was stated that the borer was thought to have entered Ohio from Ontario, Canada. However, the first infestation observed in the United States centered around Boston, Massachusetts. The two infestations are thought to have originated from two distinct introductions from two widely separated localities in Europe. The Massachusetts borers were characterized by a multivoltine behavior with two or three generations per year and had a wide range of food plants. The Ontario-Ohio borers on the other hand were characterized by a univoltine or single generation behavior and were essentially restricted to corn as a food host. In early infestation years, when Ohio borers were taken east and reared in a Massachusetts environment, they continued to have a single generation per year as they did in Ohio. Likewise, when Massachusetts borers were brought to Ohio, they continued to have 2 or 3 generations per year as they did in Massachusetts. This has led investigators to the conclusion that there are two biological species or strains in the United States. Some investigators have been inclined to explain the changes that have occurred in Ohio by saying that there must have been an introduction of the Massachusetts or multivoltine strain into Ohio, and that this strain was superimposed over the univoltine strain and tended to replace it or fuse with it.

During the period of the change in the number of generations in Ohio, Arbuthnot, in 1937, began an investigation on the genetics of the species. After 4 years of study he came to the conclusion that there were indeed two distinct biological strains in the United States. He found that the Massachusetts strain was homozygous for multivoltine behavior, that is, all of the insects continued to reproduce without a diapause as long as weather conditions permitted. The Ohio strain, on the other hand, was found to be heterozygous with a complex of multiple and single generation behavior. A homozygous single generation strain was isolated from the Ohio material, but attempts to isolate a homozygous multiple generation strain were unsuccessful; that is, some of the progeny of two-generation borers in Ohio always failed to complete two generations the following year, but entered a diapause. In cross breeding the two so-called strains, Arbuthnot found that there appeared to be somewhat of an inter-racial inhibition to mating and thought it might be due to undiscovered physical differences. However, he was able to get fertile eggs and to rear young. He found that heterosis, or hybrid vigor, was evident in the F_1 generation and resulted in a high survival, but that in the F_2 generation level mortalities were very high. In general, the progeny showed a behavior intermediate between that of the parent stocks. The larvae developed more rapidly than the parent univoltine stock but less rapidly than the multivoltine stock.

As a result of his investigations, Arbuthnot apparently came to the conclusion that the heterozygous Ohio population had come about from the mixing of two strains. In a concluding paragraph he stated that, "in the United States where the strain best suited to survive in an environment spreads into a region after a strain less well adapted to that environment has been present for several years, the strain best suited for that environment will become more abundant".

Babcock who, during the period 1924-27, studied the ecology and behavior of the species at various points in Europe, including Russia, came to a somewhat different conclusion. He found considerable variation in the behavior of the insect in different localities. He concluded that "Individuals having different seasonal cycles are not biological species in the ordinary acceptance of the phrase. After continued impress by a normal climate, the insect develops a rather stable response to this rhythm which is not immediately lost when the impress originally producing it is removed, nor is it visibly altered in every case during short periods of climatic fluctuation......The insect's physiological constitution has several distinct optima, but the optimum for the species considered as a whole seems to be the one-generation type of seasonal history. Of great importance in the direct correlation of the environment with the seasonal development of the insect is that after this adaptation has continued for a certain period of time, like intensities of factors stimulating the organism do not affect it to the same degree as before."

Babcock's opinion that the single-generation behavior is optimum for the species seems to be substantiated by the general decrease in borer population that has occurred in Ohio since the two-generation behavior developed. Most investigators agree that at the present time between 80 and 90 per cent of the borers taken in corn fields in the fall are second generation borers. Whether or not this means that the multivoltine type of behavior will completely replace the old univoltine type in Ohio because it is better fitted for the environment remains to be seen, but if such a change does occur, in the writer's opinion it will not necessarily mean that the species is more perfectly adjusted to our dent corn environment as a result of the change.

The effect of climate on the incidence of diapause or conversely on the emergence of moths for a second generation is shown in Table 1 where the percentage of moth emergence from early-planted and early-maturing sweet corn fields is given for five localities across the state from south to north.

It may be noted that emergence of moths for a second generation was highest at Cincinnati in the extreme southern part of the state and lowest

Table 1.—Average per cent of emergence of moths for a second generation from early-maturing sweet corn fields.

Locality	No. fields observed	Borers observed	Per cent emergence
Cincinnati	3	308	73.7
Dayton	2	157	63.1
Columbus	1	34	50.0
Van Wert	1	27	25.9
Elyria	3	403	22.6

at Elyria in the northern part with a direct progression downward from south to north.

A similar moth behavior is shown in records taken from plantings of the dent corn hybrid, Iowa 939, made on the same date at Cincinnati and Washington Court House (Table 2).

Table 2.--Per cent of borer emergence for a second generation from two fields of the dent corn Hybrid Iowa 939 located at Cincinnati and Washington Court House, both planted on May 1.

Locality	Borers observed	Per cent moth emergence
Cincinnati	64	45.6
Washington Court House	47	31.9

Again it may be noted that emergence was highest at the most southerly point, Cincinnati, which in latitude is about 40 miles south of Washington Court House. It is also interesting to note that moth emergence was lower in the dent corn than in the sweet corn for similar latitudes as shown in a comparison of Tables 1 and 2, thus indicating that nutrition was probably a factor influencing moth emergence. Although Iowa 939 is very susceptible to corn borer infestation, it is still not as favorable a host as are the short-season sweet corns.

In a similar study two varieties of sweet corn, Carmelcross and Ioana, differing about 10 days in maturity, were both planted in replicated plots at Dayton, Ohio, on April 25. On August 12, after corn borer growth and metamorphosis had stopped, representative stalks were dissected to determine the extent of moth emergence from the two varieties. The results are shown in Table 3.

Table 3.--Moth emergence record from two varieties of sweet corn planted on April 25 at Dayton, Ohio.

Variety	Borers observed	Per cent moth emergence
Carmelcross	103	73.8
Ioana	54	42.6

It may be noted that the shorter seasoned Carmelcross had about twice the number of borers the Ioana variety had and the Carmelcross also had a much higher moth emergence record. The Ioana variety matured about 10 days later than the Carmelcross. Although neither of these varieties can be considered resistant to corn borer infestation, it is interesting to note that the shorter-season strain, which accordingly was more susceptible to corn borer survival, also produced the most moths.

Even among dent corn plantings there have been marked differences in the number of moths that have emerged from different hybrids, depending apparently on the resistance or susceptibility of the respective strains grown. In Table 4 is shown the borer infestation and the resulting moth emergence for a series of single-cross hybrids grown in a strain performance test at Van Wert, Ohio.

Table 4.--Borer infestation and moth emergence records from six single-cross hybrids grown at Van Wert in a field test under natural infestation.

	Corn borer injury rating[1]	Total borers in 20 plants	Number in diapause	Number emerged	Per cent emergence
WF9 x 461-3	4.5	42	23	19	45.2
WF9 x 38-11	4.0	39	26	13	33.3
Oh28 x 461-3	4.0	36	24	12	33.3
Hy x WF9	2.4	27	19	8	29.6
Hy x L317	1.3	20	17	3	15.0
K155 x L317	1.0	19	19	0	0.0

[1]Rated from 1 = least injury to 5 = most injury.

The single cross hybrids in Table 4 are arranged from highly susceptible to highly resistant. It may be noted that moth emergence is directly correlated with strain susceptibility, that is, the hybrids with a high borer injury rating and high borer population also had high per cent moth emergence records. The data therefore indicate again that moth emergence was directly and strongly influenced by nutrition.

The greater per cent of summer moth emergence that has occurred in southern as compared with northern Ohio in sweet corn as compared with dent corn, and in susceptible dent-corn hybrids as compared with resistant hybrids suggests that food and climate may have had a part in selection pressure in favor of multi-generation borers. Such climatic and host effects are not unprecedented in insect life. Steinberg and Kamensky in France found that temperature and food affected the incidence of diapause in *Loxostege sticticalis* (L.) (Lepidoptera, Pyralidae). Pictet bred the species *Lasiocampa quercus* L. (Lepidoptera, Pyralidae) for 6 generations at a constant temperature of 22° C. Although in the first generation all of the insects hibernated for the full period, in successive generations the length of the hibernation period was gradually diminished. By the fifth generation 18 per cent developed without a diapause and 52 per cent were inactive for only a month. In the sixth generation, practically all of the individuals transformed without a diapause. In commenting on Pictet's work Uvarov in his treatise on Insects and Climate made the statement that Pictet's experiments support the idea that "the life cycle of a species can be directly influenced by the seasonal climatic cycle. Indeed, since only 6 generations were necessary to produce a substantial change in the life cycle, in adjustment to the new conditions, it is reasonable to suggest that a climatic cycle acting on a species for countless generations may make the species perfectly adjusted to it." The occurrence of the two-generation behavior all over the midwest within a very few years time tends to preclude the possibility of a new introduction being responsible for the change. If it took 25 years for the first introduction to spread to a given area of distribution, why should a new introduction cover the same territory in 2 or 3 years?

Futhermore, the corn borer throughout the midwest area retained its restriction to corn as the favored host. Even after the change from the univoltine to the multivoltine type of behavior it has not accumulated in large numbers in weed areas as has always been true of the multivoltine form in the New England area. Occasional infestations are seen in potatoes, peppers, gladiolus, and a few other plants, but such infestation occurs only when corn is not available or not in the attractive stage for oviposition. Borers may be taken commonly in various weeds in and around corn fields, but these individuals may usually be considered migrants from corn plants on which the eggs had been deposited.

The evidence, therefore, indicates that the change in the behavior of the insect in Ohio and the midwest has come about as an adaptation to the climatic conditions and the food relationships. Apparently the insect at the time of its introduction into Ohio retained in its genetic makeup a tendency toward multivoltine behavior that only attained its expression after exposure to conditions favorable to change had occurred. Wishart (1947) makes the statement, "The increase in the multivoltine habit (in Canada) is not due to the introduction of the true multivoltine race from New England but to an increase in a tendency which has been present in the one generation population over a long period." The writer of this article is of the same opinion as to the change in behavior that has occurred in Ohio and suggests that the change has come about as an adaptation to climate and food.

The change in the behavior of the insect seems to have reduced its potentiality for injury to the corn crop in Ohio. The first generation now attacks the crop too early for maximum accumulation and damage and the second generation comes after the crop is nearing maturity and hence is fairly well made. At any rate Ohio farmers are not nearly as much concerned about the possibility of corn borer damage to the main corn crop today as they were 20 years ago. How much of this change of attitude has come about as a result of improved cultural practices, better and more corn borer resistant hybrids, and the introduction and accumulation of corn borer parasites and predators is an open question. But in the writer's opinion the change in the behavior of the insect has had a share in the alleviation of the problem in Ohio.

In conclusion, it must not be understood that the corn borer is now relegated to a minor position in the corn production program. It is still the major corn insect problem of the United States and will undoubtedly continue to cause important damage, the extent of which will depend upon the ecological conditions operative at the time. During the past 20 years, injury from the first generation in Ohio has been much less than that formerly caused by the single generation. The second generation has not made up the difference. Perhaps in future years, climatic conditions will sometimes favor the first generation and sometimes the second and the relative importance of the two generations will consequently vary. If conditions highly favorable to both generations should occur in any one year, high populations and severe damage may result. However, as long as the present behavior of the insect persists, it is not expected that the corn borer will be the major calamity that was once anticipated.

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